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BLOWFLY FLIGHT AND OPTIC FLOW

II. HEAD MOVEMENTS DURING FLIGHT

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Summary

The position and orientation of the thorax and head of flying blowflies (*Calliphora vicina*) were measured using small sensor coils mounted on the thorax and head. During flight, roll movements of the thorax are compensated by counter rolls of the head relative to the thorax. The yaw turns of the thorax (thorax saccades) are accompanied by faster saccades of the head, starting later and finishing earlier than the thorax saccades. Blowfly flight can be divided into two sets of episodes: ‘during saccades’, when high angular velocities of up to a few thousand degrees per second are reached by both the thorax and head, and ‘between saccades’, when the orientation of the thorax and,

in particular, the head is well stabilized. Between saccades, the angular velocities of the head are approximately half those of the thorax and lie mostly in the range $0\text{--}100^\circ\text{s}^{-1}$ for any rotation (yaw, pitch and roll). These velocities are low enough to limit the visual blur attributable to rotation. It is argued that the split into periods during which either rotational optic flow (‘during saccades’) or translatory optic flow (‘between saccades’) dominates is helpful for processing optic flow when signals and neurons are noisy.

Key words: *Calliphora vicina*, saccade, search coil, optic flow, three-dimensional eye movements, blowfly.

Introduction

Blowflies are well-known for their agility during flight, performing fast and acrobatic flight manoeuvres. This flight behaviour must have important consequences for vision. First, fast turns can lead to motion blur, impairing vision of spatial details (Srinivasan and Bernard, 1975). Second, turns interrupt the pattern of optic flow that reveals the three-dimensional structure of the surroundings during translation (Koenderink, 1986). In principle, these adverse effects of flight behaviour can be alleviated by compensatory eye movements (Carpenter, 1988; Land, 1973, 1975; Steinman and Collewijn, 1980).

For blowflies, with their compound eyes fixed to the head, these eye movements correspond to head movements. The head of blowflies has appreciable freedom of movement because the neck is flexible and controls head posture *via* an elaborate system of muscles (Strausfeld et al., 1987; Hengstenberg, 1992). Experiments on tethered flies show that head movements can indeed be used to partly compensate thorax rotations (roll, Hengstenberg et al., 1986; Hengstenberg, 1992; yaw, Land, 1973, 1975). In the studies of Land (1973, 1975), thorax rotations in the yaw direction (rotation around a vertical axis) occurred in fast steps (called thorax saccades). Between these saccades, the thorax and, in particular, the head were more stable. These experiments were subsequently challenged by Geiger and Poggio (1977), who argued that the saccadic behaviour was an artefact attributable to the appreciable mass and inertial momentum added to the animal

by the tether. Using a lighter tether, they were unable to repeat the observations of Land (1973, 1975). Subsequent measurements on insects in free flight, however, have supported the existence of thorax saccades at least (*Syrphia pipiens*, Collett, 1980; *Musca domestica*, Wagner, 1986). Unfortunately, using the techniques available (video and film), these experiments were unable to resolve head movements, gave little or no information on roll movements and had a rather low temporal resolution (typically 20 ms).

With the development of a modified search coil technique suitable for measuring position and orientation in (almost) freely flying blowflies (Schilstra and van Hateren, 1998a,b, 1999), it has now become possible to re-address this question of how the head and thorax move during flight. The new technique was developed specifically to provide information about the spatiotemporal input received by the blowfly eye during normal flight: this input can be reconstructed from the stimuli on the walls of the flight cage and from the measured eye positions and orientations. The statistical properties of this input play an important role in recent theories of early visual processing (see van Hateren, 1992a,b). A full analysis of this input is beyond the scope of the present article, however. Instead, we will concentrate on the detailed properties of the head movements occurring during thorax saccades (see Schilstra and van Hateren, 1999). It is shown that the free-flight behaviour of blowflies can be separated into two sets of

episodes ('during saccades' and 'between saccades'), which have very different patterns of rotational optic flow.

Materials and methods

Position and orientation measurements

The position and orientation of flying blowflies were measured as described by Schilstra and van Hateren (1999) (for further details of the methods, see Schilstra and van Hateren, 1998a). Briefly, pairs of coils surrounding the flight cage (40 cm×40 cm×40 cm) generate magnetic fields that induce voltages in small sensor coils attached to a blowfly (a female *Calliphora vicina*). These voltages are transferred *via* a thin cable, hanging down from the fly's abdomen, to amplifiers and can be used to calculate the fly's position and orientation for each millisecond. In the study of Schilstra and van Hateren (1999), coils were attached to the thorax, but in the present study they were either attached to the head only (Fig. 1A) or to both the thorax and the head (Fig. 1B), using two sets of sensor coils and amplifiers. The coils attached to the head were lighter (0.8 mg, 40 windings of 2 mm diameter) than those attached to the thorax (1.6 mg, 80 windings of 2 mm diameter). The size of the head coils was chosen as a reasonable compromise to give an adequate angular resolution (signal-to-noise ratio) without significantly disturbing the head motion (see Results for control experiments). As shown in Fig. 1, the cable passed from the head coils to the thorax *via* a loop (height 8–10 mm), which was flexible enough to enable virtually unrestrained head movements (see Results for control experiments). As in the study of Schilstra and van Hateren (1999), the walls of the flight cage were covered with photographs of natural scenes, and the luminance was 150 cd m⁻² for the walls and 800 cd m⁻² for the ceiling.

Preparations and flight recordings

Preparations for attaching the coils to the head were similar to those described for the thorax (Schilstra and van Hateren, 1999). On the dorsal side of the head, hairs hindering mounting of the coils were cut away, and the coils were glued in position using a tiny amount of (viscous) cyanoacrylate adhesive. The

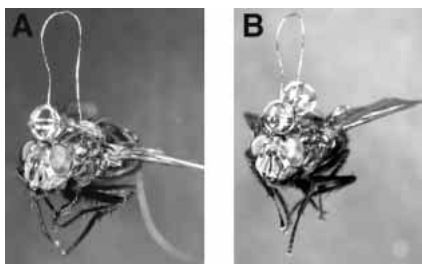


Fig. 1. (A) A blowfly with coils mounted on the head. The wire loop provides freedom of movement for the head. The wire runs *via* the thorax and abdomen to the bottom of the flight cage. (B) A blowfly with coils mounted on the head and thorax. All 2×6 degrees of freedom are measured simultaneously using two sets of nine lock-in amplifiers each.

position of the coils was such that only a small part of the field of view of the compound eyes was restricted. This restriction appears to induce no measurable changes in thorax and head movements, as indicated by experiments with different coil sizes (1, 2 and 3 mm), restricting different amounts of the field of view. The coils restrict the field of view of the ocelli (three single-lens eyes on top of the head) more severely, although not completely. The influence of this on thorax and head movements was probably also small: first, because we found no differences in (thorax) flight behaviour between flies with or without head coils and, second, because the role of the ocelli in determining head posture appears to be negligible (Schuppe and Hengstenberg, 1993).

The orientation of the coils was estimated, and deviations from the standard orientation were corrected in the final reconstruction. This yielded angles relative to an orthogonal coordinate system fixed to the head. This system is defined by a plane parallel to the chitinous surface at the back of the head capsule and the plane of symmetry of the head. The position of the head is calculated as the origin of the head coordinate system, a point approximately midway between the compound eyes.

The cable forming the loop coming from the head coils was glued to the thorax, led to the abdomen and glued to either the last or the second to last segment. For experiments with a second set of coils (on the thorax), the second cable was also glued to the abdomen. The two cables running to the bottom of the cage were loosely twisted to keep them together during flight.

For most of the analysis described below, the results of experiments on four flies with coils on both the head and thorax were used. The head movements measured in these experiments were consistent with experiments on 13 flies for which only head movements were measured. Moreover, control experiments were performed (with various coil configurations) on another 17 flies. For the averages and probability density histograms presented in Figs 4–6, only flights lasting at least 2 s were selected, yielding a total flight time of 703 s containing 6697 (detected) saccades.

Angular coordinates

Angles are defined according to a Fick system (see Haslwanter, 1995), in which the orientation of an object is given by a rotation matrix formalizing an ordered sequence of yaw, pitch and roll rotations of the object (see Fig. 3, inset). The rotation matrix describes the orientation of an object relative to a fixed, external coordinate system, which will be called the laboratory system. In addition, the angular orientation of the head is also given relative to the thorax. This is calculated by multiplying the inverse of the thorax rotation matrix by the head rotation matrix (Haslwanter, 1995). Angular velocities are not calculated in the laboratory coordinate system, but in the coordinate systems rotating with either the thorax or the head. These velocities are obtained from the (differential) rotation matrix describing the rotation of, for example, the thorax from one millisecond to the next. Once

this rotation matrix has been obtained, the yaw velocity, pitch velocity and roll velocity are easily calculated (using equation A4 of Haslwanter, 1995). From the differential rotation matrix, it is also possible to calculate the rotation velocity vector (analogous to equations 23 and 25 of Haslwanter, 1995), which then yields the total angular velocity (analogous to equation 22 of Haslwanter, 1995). Finally, from the angular velocities in the thorax and head coordinate systems, the corresponding angular accelerations can be obtained by differentiation with respect to time.

Results

Mounting coils on the head rather than on the thorax increases the risk of artefacts. Not only is the mass ratio worse (coils:head 0.8:8; coils:thorax 1.6:80), but the extra load on the neck muscles due to the loop connecting the head and thorax may also be a problem. Therefore, a series of control experiments was performed to assess the extent of the mechanical disturbance attributable to the coils and loop. The results from these experiments are presented first, and the results of the free-flight experiments are described subsequently.

Control experiments

Two types of experiment were designed to estimate the effects of the sensor coils and cable loop on the head motion of the fly. The first experiment determines whether the stiffness of the cable loop running from the head to the thorax affects head motion. The second experiment investigates how much mass can be added to the head before normal head motion is significantly disrupted. Both experiments were based on measurements of the compensatory head roll reflex of blowflies: when the thorax is suddenly rolled, the head rolls partly back after a short delay (Hengstenberg et al., 1986; Hengstenberg, 1992). A tether was glued to the dorsal part of a fly's thorax, and the fly was suspended such that it could be rotated around its long axis without changing its position. The fly was placed inside a Perspex cylinder (diameter 6 cm, length

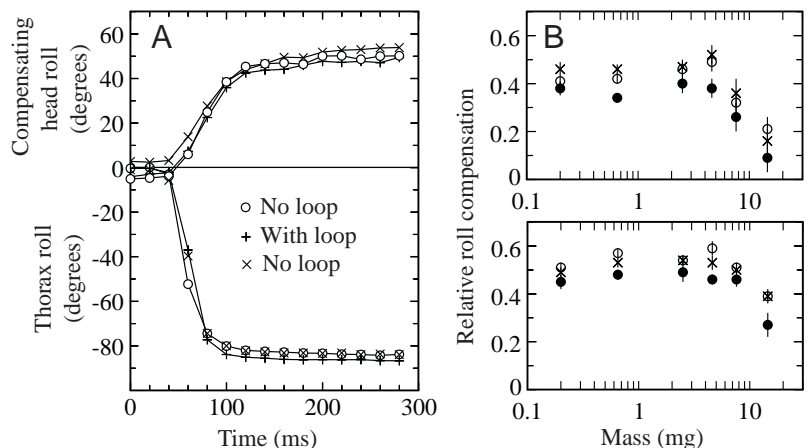
18 cm), of which the lower half was covered with black paper and the upper half with frosted paper, brightly lit from the outside. Despite the tether, flies usually tried to fly for periods of variable duration. During such flight, the fly was occasionally subjected to an abrupt roll of 90° .

In the first experiment, movements of the head and thorax were both recorded on video at a rate of 50 fields s^{-1} (a field is equal to a half-frame). Compensatory head rolls were recorded for a series of thorax rolls, both with and without the cable loop running from the head to the thorax, but without any additional mass (i.e. no coils). Segments of the video recording were digitized, converted to a series of graphics files and subsequently analyzed field by field using a public domain graphics browser (Paint Shop Pro). From these measurements, the thorax roll (relative to the laboratory) and the compensatory head roll (relative to the thorax) were determined. Fig. 2A shows an example of the measurement so obtained. First, no loop was present (open circles, average of five rolls), then a loop was attached to the head and thorax of the same animal, and the experiment was repeated (plus symbols, average of 10 rolls), and finally the loop was removed (crosses, average of four rolls). The presence of the loop has no discernible effect on the compensatory roll reflex: both with and without the loop, the head compensates approximately 50% of the thorax roll, with a delay of a few video fields (of 20 ms each). The head roll reflex we find here is similar to that reported by Hengstenberg et al. (1986) and Hengstenberg (1992). We performed this experiment on two other flies and consistently found no effects of the loop on the head roll reflex. Furthermore, we observed that manually moving the (loosened) thorax end of the loop over realistic distances had a negligible effect on the head position. We conclude that the stiffness of the loop is low enough for the present purpose.

In the second control experiment, the head orientation (again in tethered flies) was measured at a rate of 1 kHz with a very lightweight system of sensor coils attached, made of coils with 20 windings and a diameter of 1 mm. The total system had a mass of approximately 0.2 mg (cf. 8 mg for the head). Movements were also recorded on video tape, enabling a *post-*

Fig. 2. Control experiments for measuring the influence of the coils and loop on normal head movements. (A) Imposed thorax roll (relative to the laboratory) and compensatory head roll (relative to the thorax) measured from analyses of video recordings of a tethered fly. The open circles show the response when the head is completely free, the plus signs show the response with a loop connecting the head and thorax (but no coils present) and the crosses show the response after the loop has been removed. (B) Relative roll compensation (the size of the compensatory head roll divided by the size of the thorax roll) as a function of the mass mounted on the head. Measurements were made with lightweight sensor coils; the symbols show the roll compensation at different times after the thorax roll: 50 ms (filled circles), 150 ms (crosses) and 450 ms (open circles).

Upper graph, rolls to the right; lower graph, rolls to the left. See text for further explanation. Values are means \pm S.D., $N=20-40$.



hoc visual check on the head roll reflex and on when the fly had been flying. Small pieces of metal with different masses were subsequently attached to the head by sticking them to a tiny amount of grease, and the compensatory head roll was measured. Fig. 2B shows the results for rolls of approximately 90° to the right (upper panel, average of 20–40 rolls) and to the left (lower panel, average of 20–40 rolls). The relative roll compensation (the size of the compensatory head roll divided by the size of the thorax roll) is given at three times after the start of the thorax roll: 50 ms (filled circles), 150 ms (open circles) and 450 ms (crosses). The difference between leftward and rightward compensation lies within the normal variation one finds for the roll compensation: this varies somewhat between flies, and even for a single fly it may vary as a function of time or roll direction. As can be seen from the roll compensation as a function of the added mass, the roll reflex is only disturbed for the largest masses (7.6 mg and 14.5 mg). In these cases, we also observed, in the traces with 1 ms resolution, transient artefacts immediately after the initiation of the thorax roll. For the smaller masses (0.2, 0.65, 2.5 and 4.6 mg), the compensatory head rolls were free from this artefact and were all similar. It therefore appears that the blowfly head has a certain amount of mechanical reserve to carry and move loads in excess of its own mass (8 mg). For rotation, it is not just the mass, but rather the added inertial momentum, that is important. Because the coils are mounted on top of the head, this problem is larger for roll and pitch movements than for yaw movements (because in the latter case the axis of rotation goes approximately through the centre of mass of the coils, minimizing the effective inertial

momentum). From the observation that the roll movement is only affected for larger masses, we conclude that the mass of the standard coil system used for the head (0.8 mg) is not expected to have a large influence on head rotations. Nevertheless, we show below (see *Head pitch oscillations*) that there are subtle effects on the small head oscillations in the pitch direction that are induced by the wing beat.

Angular motion of the head and thorax

Head and thorax rotations during a typical blowfly flight are shown in Fig. 3. The upper panel shows the saccadic behaviour of both the thorax (thin blue lines) and the head (thick red lines). At a rate of approximately 10 s^{-1} , the yaw (rotation around a vertical axis, see inset) changes abruptly. The size of the steps in yaw varies: most of the steps are small (up to several tens of degrees), but larger steps of up to 90° occur occasionally (Schilstra and van Hateren, 1999). The head saccades are generally faster than the accompanying thorax saccades (Schilstra and van Hateren, 1998b), starting later and finishing earlier (see insets for examples; see below for averages).

The middle panel of Fig. 3 shows the pitch (up–down rotations). Steps in pitch usually occur simultaneously in the thorax and head. Between steps, the pitch is slightly more stable for the head than for the thorax (see, for example, the traces at approximately 1000 ms). Furthermore, the head is held more level than the thorax: the latter is kept at a pitch of approximately 30° during flight. Much of the variation in thorax pitch has to do with varying the direction of the flight force, thus producing variations in forward and vertical speed.

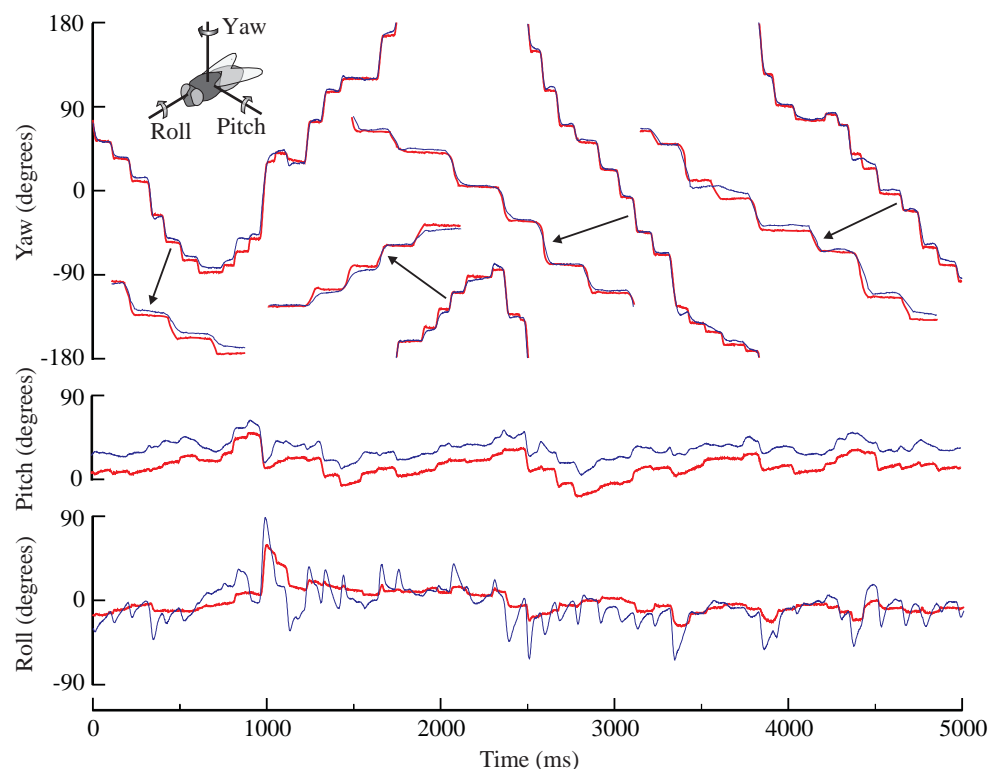


Fig. 3. Angles during a typical blowfly flight. Thin blue lines denote thorax movement, and thick red lines denote the corresponding head movement. Yaw, pitch and roll are defined as shown in the inset. Further insets show enlarged views of yaw saccades ($2.5\times$ horizontally, $1.5\times$ vertically). Note that the head saccades are generally shorter than the corresponding thorax saccades and that the roll of the head is typically much smaller than the roll of the thorax. A movie showing a reconstruction of thorax and head movements can be found at http://hlab.phys.rug.nl/demos/flying_eye.

The lower panel of Fig. 3 shows the roll (rotations around the length axis of the animal). The thorax makes fast and large roll movements during flight, because they are required to make turns (similar to the roll an aeroplane has to make when changing course; see Schilstra and van Hateren, 1999). The head roll, in contrast, is quite modest for most of the time because most of the thorax rotation is effectively compensated by counter rolls of the head relative to the thorax (for similar results on tethered *Calliphora* spp., see Hengstenberg et al., 1986; Hengstenberg, 1992; for results on blowflies in free flight, see Schilstra and van Hateren, 1998b). Very large thorax rolls sometimes (but not always) result in some residual roll of the head.

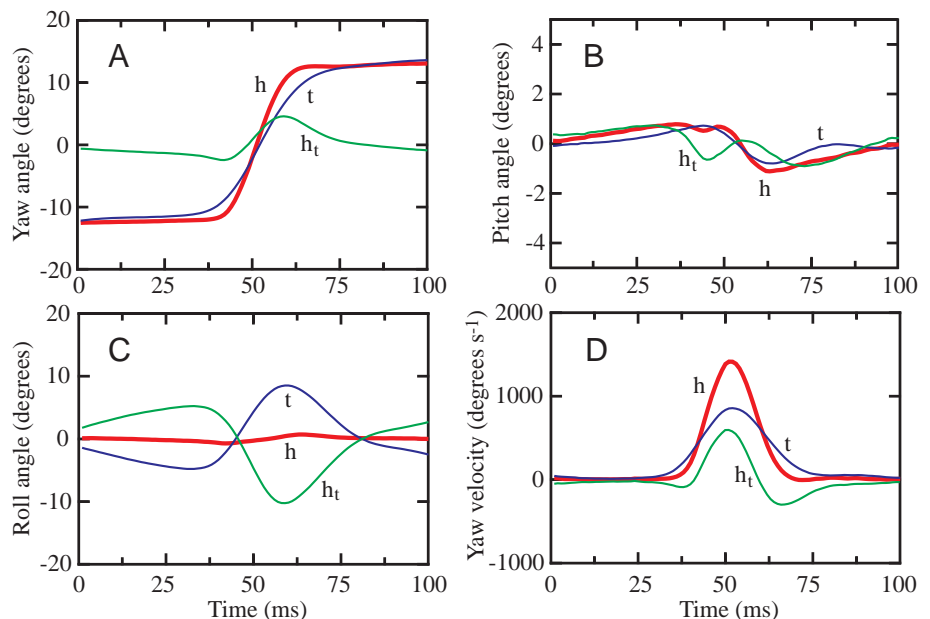
Saccades can be detected from peaks in the total angular velocity of the head. Fig. 4 was obtained by averaging the various angles and angular velocities over a stretch of 100 ms surrounding the detection point; this was performed here for saccades with a yaw of 20–30° to the right. Fig. 4A shows the resulting yaw for the thorax (t), the head (h) and the head relative to the thorax (h_t). The yaw of the thorax starts to change first, whilst the head is kept stable by a counter rotation of the head relative to the thorax. After approximately 10 ms, the head starts to move, faster than the thorax, and reaches its final orientation well before the thorax. This is accomplished during the final stages of the turn again by a counter rotation of the head relative to the thorax.

The pitch (Fig. 4B) changes, on average, very little during a saccade (note the difference in scale between Fig. 4A and B). The residual movement of the head is typically concentrated at the time when the yaw velocity is high. The roll (Fig. 4C) is entirely different from the yaw: here, the head is not working with, but against, the thorax. The head performs a counter rotation (h_t , head relative to thorax) effectively compensating the thorax rotation (t), leading to only small residual roll movements of the head with respect to the outside world (h).

The angles for the head and thorax in Fig. 4A–C are given relative to the laboratory coordinate system. For flight control, as performed by the fly's sensors and muscles, however, the coordinate systems defined by the thorax and the head are at least as important. These coordinate systems are fixed to the thorax and head, respectively, and move and rotate along with them. A yaw in the thorax coordinate system implies a torque produced by the wings around a well-defined axis of the thorax. Therefore, it can be produced, at least in principle, by a fixed program of muscular activity. The coordinate system of the head is identical to the coordinate system of the compound eye. This is the preferred system for assessing the blur caused in the compound eye by the various rotations. Furthermore, this system clarifies the visual consequences of rotational optic flow for the various visual interneurons.

Since the thorax and head coordinate systems are continuously changing in orientation, they cannot yield absolute values for the yaw, pitch and roll coordinates themselves (there is no fixed scale for these coordinates). What can be calculated unambiguously, however, are differential measures, i.e. angular velocities and angular accelerations. The current yaw velocity of the thorax, for example, is then defined as the yaw rotation per millisecond needed to rotate the thorax from its coordinate system 1 ms ago to the present thorax rotation. The yaw acceleration is the derivative with respect to time of the yaw velocity; it is proportional to the torque that must have been present around the yaw axis of the thorax (because torque = inertial momentum \times angular acceleration). Fig. 4D shows an example of the yaw velocities of the thorax (t, in the thorax coordinate system), the head (h, in the head coordinate system) and the head relative to the thorax (h_t , in the thorax coordinate system). Again, we see that the head rotates in a shorter time and at a greater velocity than the thorax.

Fig. 4. Mean angles and angular velocities of 620 saccades to the right, with a yaw of 20–30°. (A) Yaw of the thorax (t), the head (h) and the head relative to the thorax (h_t). (B) As in A, for the pitch. (C) As in A, for the roll. (D) Yaw velocity of the head (h, measured differentially relative to the head coordinate system), of the thorax (t, relative to the thorax coordinate system) and of the head relative to the thorax coordinate system (h_t ; this is the rotation per unit of time required to go from the previous head orientation relative to the previous thorax orientation to the current head orientation relative to the current thorax orientation).



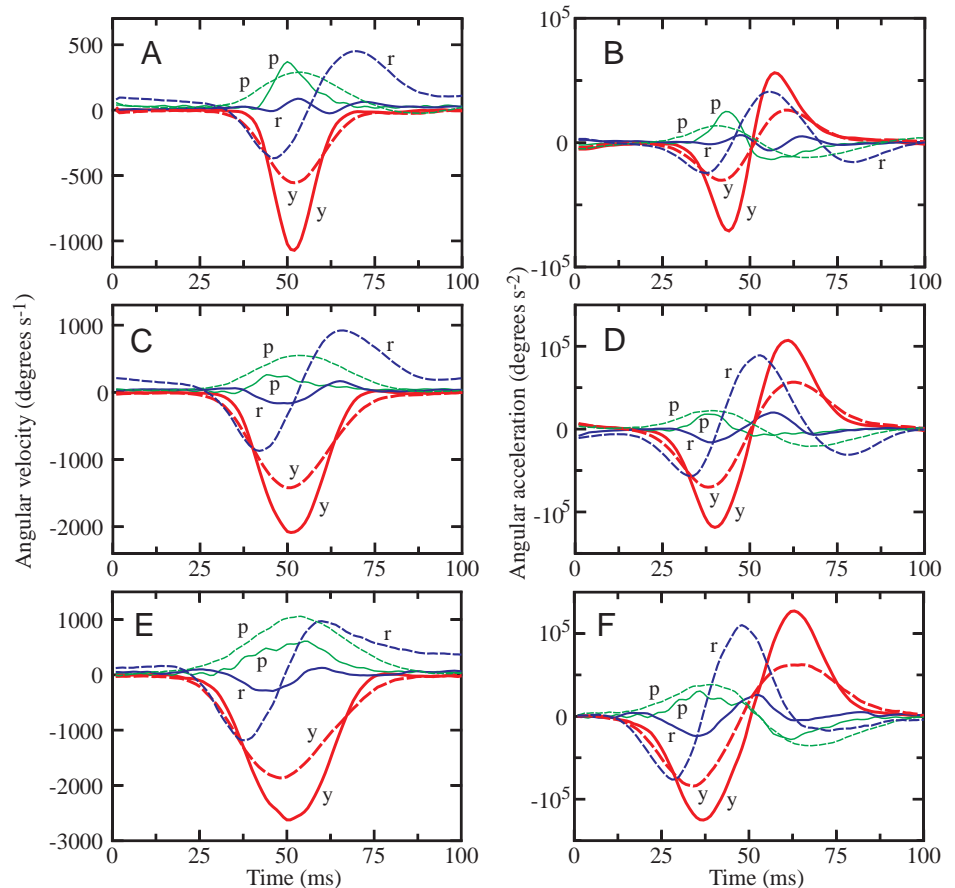


Fig. 5. Angular velocities and accelerations of the head (continuous lines) and thorax (broken lines); for the head, these are measured relative to the head coordinate system; for the thorax, these are measured relative to the thorax coordinate system; y, yaw; p, pitch; r, roll. (A,B) Average of 722 saccades with a yaw of $10\text{--}20^\circ$ to the left. (C,D) Average of 449 saccades with a yaw of $30\text{--}40^\circ$ to the left. (E,F) Average of 112 saccades with a yaw of $60\text{--}70^\circ$ to the left.

Angular velocities and accelerations during a saccade

Mean angular velocities and accelerations are shown in Fig. 5 for yaws (to the left) of $10\text{--}20^\circ$ (Fig. 5A,B), $30\text{--}40^\circ$ (Fig. 5C,D) and $60\text{--}70^\circ$ (Fig. 5E,F). Yaws to the right give similar results, and yaws of intermediate sizes give intermediate curves. The broken lines denote thorax movements, and the continuous lines denote head movements. The yaw (y) of the head starts later, stops earlier and reaches higher speeds than the yaw of the thorax. For small saccades, this difference in speed is approximately a factor of two, which implies that the neck muscles contribute about as much to the angular speed of the head as is contributed by the flight muscles rotating the thorax. For larger saccades, the increased angular velocity and acceleration of the head are produced exclusively by an increase in thorax velocity and acceleration. The yaw velocity of the head relative to the thorax is approximately constant ($684 \pm 92^\circ \text{ s}^{-1}$, mean \pm S.D.) for saccades larger than 20° . The yaw acceleration of the head relative to the thorax also reaches a plateau for saccades larger than 20° ($5.1 \times 10^4 \pm 0.6 \times 10^4^\circ \text{ s}^{-2}$).

Whereas the pitch (p) velocity of the thorax increases with increasing saccade size (Schilstra and van Hateren, 1999), the pitch velocity of the head is more variable. The duration of pitch movements of the head is generally shorter than that of pitch movements of the thorax. As can be seen in Fig. 5, the pitch movement of the head shows a clear ripple, with a

frequency close to the wingbeat frequency (between 120 and 170 Hz in blowflies). This pitch ripple will be discussed further below.

The roll (r) velocity and acceleration of the head are much reduced compared with those of the thorax. The roll velocities of the head relative to the thorax increase along with the roll velocities of the thorax to values of $1000\text{--}1200^\circ \text{ s}^{-1}$ for large saccades. The maximum acceleration of the head relative to the thorax ($8.6 \times 10^4 \pm 0.6 \times 10^4^\circ \text{ s}^{-2}$) is almost as large as that reached by the thorax during large saccades (approximately $10^5^\circ \text{ s}^{-2}$; see Schilstra and van Hateren, 1999).

Stabilizing gaze

The thorax and head movements made by blowflies during flight have consequences for the functioning of the fly's visual system. It is useful to distinguish two different sets of episodes, the first consisting of the periods surrounding the point at which the thorax makes a saccade, and the second consisting of the periods between saccades. From Fig. 3, for example, it is clear that such a distinction can be made: the saccades are sharp and short, and they demarcate periods of more stable angular orientation. Between saccades, this stability is greater in the head than in the thorax for all three angles; during saccades, head stability is greatest for roll. To assess this quantitatively, we calculated probability densities of the velocities and accelerations of the yaw, pitch and roll for the

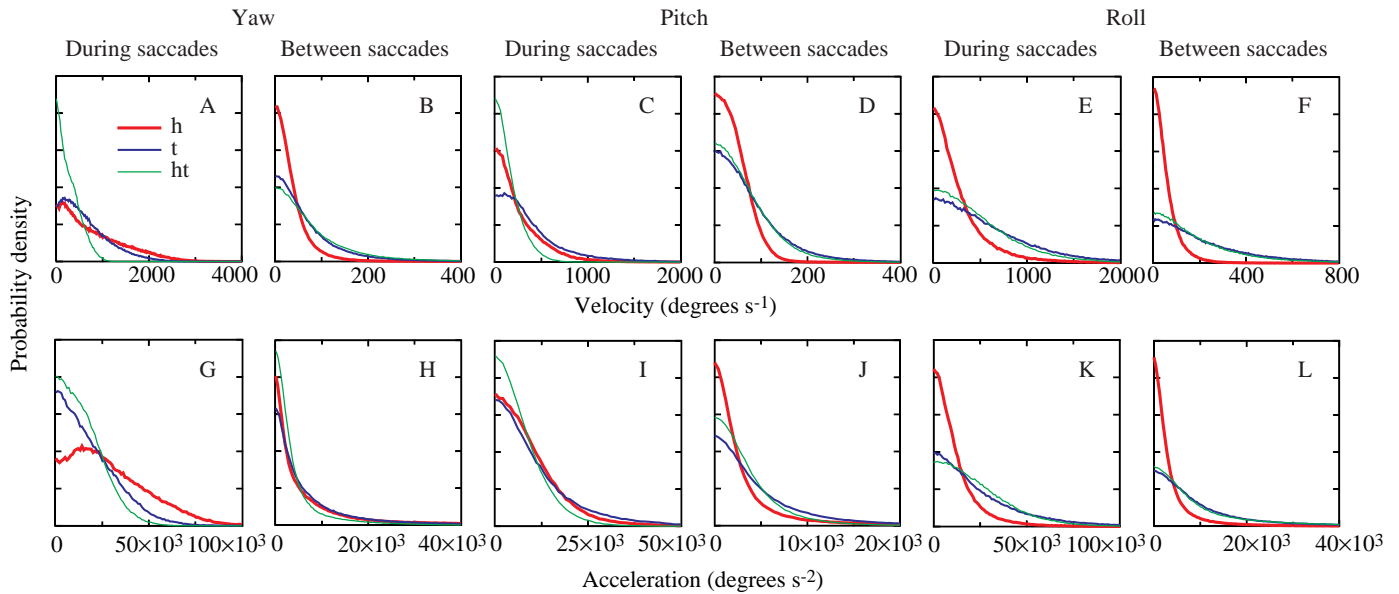


Fig. 6. Probability densities of the angular velocities and accelerations of the head (h, thick red line), the thorax (t, broken blue line) and the head relative to the thorax (ht, thin green line). The total flight time was divided into two sets of episodes, 'during saccades' and 'between saccades'; see text for further explanation. Full scales are as follows: (A) 3×10^{-3} degrees s^{-1} , (B) 2.5×10^{-2} degrees s^{-1} , (C) 5×10^{-3} degrees s^{-1} , (D) 1.5×10^{-2} degrees s^{-1} , (E) 3.5×10^{-3} degrees s^{-1} , (F) 1.5×10^{-2} degrees s^{-1} , (G) 5×10^{-5} degrees s^{-2} , (H) 2.5×10^{-4} degrees s^{-2} , (I) 10^{-4} degrees s^{-2} , (J) 3.5×10^{-4} degrees s^{-2} , (K) 8×10^{-5} degrees s^{-2} , (L) 3×10^{-4} degrees s^{-2} .

two sets of episodes (Fig. 6). Head saccades were detected from peaks in the total angular velocity of the head. Integrating this angular velocity over the entire saccade gives the length of the angular trajectory traversed by the head during the saccade. Subsequently, the times when 10% and 90% of this trajectory were completed were computed. Finally, the period between these two times was extended by 25% both at the onset and at the end, to include the early and late phases of both the head and thorax saccade. This then defined a period classified as 'during saccades'. Visual inspection of a large number of traces showed that this (somewhat heuristic) algorithm gives, irrespective of saccade size, a good estimate of the period during which the saccade unfolded. All other times (63% of the total flight time) are then defined as 'between saccades'.

Fig. 6A shows that, during saccades, the yaw velocities of the head and the thorax reach maximum values of a few thousand degrees per second. Yaw velocities between saccades (Fig. 6B) are much lower, in particular for the head relative to the surroundings (thick red line). This is accomplished by yaw velocities of the head relative to the thorax (thin green line) with a similar distribution to those of the thorax (broken blue line). This is also true for the pitch and roll velocities between saccades (Fig. 6D,F): the residual head angular velocities mostly lie in the range $0-100^\circ s^{-1}$, clearly lower than those of the thorax. During saccades, the yaw, pitch and roll velocities (Fig. 6A,C,E) are much greater than between saccades. Whereas the yaw and pitch velocities of the thorax and head are similar during saccades (Fig. 6A,C), they differ for the roll velocity (Fig. 6E). In the roll direction, the head is always better stabilized than the thorax, even during saccades.

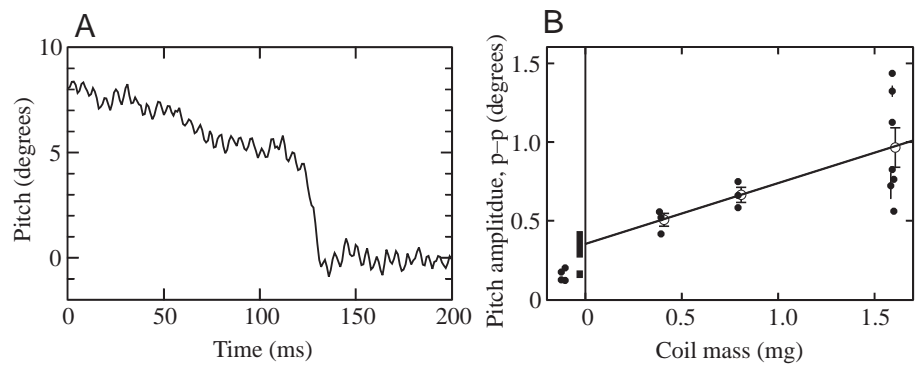
The lower row of Fig. 6 gives the accelerations corresponding to the upper row. As expected, the yaw acceleration of the head is much greater than that of the thorax during saccades. The reverse is true for roll: head accelerations are smaller than thorax accelerations, both during and between saccades. Note that the accelerations of the head relative to the thorax are generally similarly distributed to the accelerations of the thorax. This matching of effective neck muscle performance to effective flight muscle performance is a necessary requirement for effective gaze stabilization.

Head pitch oscillations

Single traces of the pitch of flying blowflies always display an oscillation with a frequency between 120 and 170 Hz and with an amplitude that varies somewhat, but is generally approximately 0.5° (peak-to-peak, see Fig. 7A). The frequency matches the wingbeat frequency of *Calliphora vicina*, and it appears that these are vibrations that are somehow transferred from the flight motor in the thorax to the head. The yaw and roll often show similar oscillations, but they are smaller and more variable. As the pitch oscillation is not as obvious in the thorax movement as it is in the head, we investigated the possibility that it was an artefact caused by the coils on the head or the loop connecting the thorax and head.

One possibility is that the loop transfers (small) vibrations from the thorax; these vibrations might be amplified if the stiffness of the loop forms a resonator with the mass of the head. We tested this possibility in tethered flies by mechanically driving the (loosened) thorax end of the loop (by attaching it to a small loudspeaker) at frequencies in the range of the wingbeat frequency. We observed no significant

Fig. 7. (A) An example of the pitch oscillation observed in the head during free flight. (B) The peak-to-peak (p-p) amplitude of the pitch oscillation as a function of total coil mass. Measurements on the head of 13 flies are plotted on the right (filled circles), and measurements on the thorax of four flies are plotted on the left (filled circles). The mean values and S.E.M. of these measurements are shown by the open circles. The line is a least-squares fit to the mean values. The lower vertical bar shows the mean and S.E.M. of the thorax oscillation amplitude, and the upper vertical bar is the linear extrapolation to coil mass zero of the head oscillation amplitude (mean \pm S.D.).



movement or resonance of the head, and we conclude that the loop is not causing the head pitch oscillations.

The only other way that the oscillations generated by the flight motor can be transferred to the head is through the neck. Pitch oscillations of the head may be produced by pitch oscillations of the thorax, but also by small oscillatory displacements of the thorax. For example, if the thorax oscillates slightly along its length axis (superimposed on its overall movement, similar to the intermittent forward motion of a rowing boat), this might cause a pitch movement of the head. This would happen if the resulting force vector, as transferred through the neck, were not acting exactly through the centre of mass of the head. Because the mass of the coils is expected to shift the centre of mass slightly upwards, the head oscillation may be a function of the mass of the coil. We tested this possibility by varying the mass of the coils and measuring the amplitude of the pitch oscillation from the surplus of power observed at approximately the wingbeat frequency in the power spectrum of the pitch. The right side of Fig. 7B shows the results for 13 blowflies (small filled circles) with coils of 1.6 mg (80 windings, diameter 2 mm), 0.8 mg (40 windings, 2 mm) and 0.4 mg (20 windings, 2 mm). Smaller coils gave too much noise to allow the amplitude of the pitch oscillations to be estimated reliably. The open circles and bars show the means and standard errors of the means of these measurements. These mean values lie close to a straight line; the continuous line is a least-squares fit to the mean values. The vertical bar to the left denotes the mean and standard deviation of this fit for a coil of zero mass. If we assume that such a linear extrapolation is justified, this analysis predicts that, in the absence of coils, the amplitude of the pitch oscillation of the head would be $0.35 \pm 0.08^\circ$ (peak-to-peak). For four other flies, with coils mounted only on the thorax, we observed that pitch oscillations also occurred in the thorax (four data points on the left of Fig. 7B), but these are smaller than those of the head. The small vertical bar denotes the mean and standard error of the mean of these measurements: $0.15 \pm 0.02^\circ$. This is significantly different from zero, but also significantly smaller than the estimated head oscillation. Some of the head oscillation may indeed be generated by oscillatory displacements of the thorax: we observed peak-to-peak

amplitudes of 50–100 μm in all directions (again determined from peaks in the power spectrum of the various displacements). However, because the dorsal part of the thorax (where the coils are mounted) is likely to move in a somewhat different manner from the neck (driving the head), no further conclusions about thorax/head mechanics can be drawn at this stage.

Discussion

During flight, head rotations of blowflies effectively compensate for part of the thorax rotations, which results in improved conditions for vision. Between saccades, stabilization of the head in all angular degrees of freedom (yaw, pitch and roll) is approximately twice as good as that of the thorax (Fig. 6). During saccades, the head compensates for most of the thorax roll, and the yaw movement of the head is shorter than that of the thorax (Figs 4, 5). As a result of these head movements, blur in the visual system is significantly reduced. Furthermore, by minimizing the duration of head rotations, rotational optic flow is minimized. The optic flow due to translation will then dominate. This type of optic flow yields, in contrast to rotational optic flow, information about the three-dimensional structure of the visual environment (through motion disparity, i.e. the differential visual speeds of objects at different distances). Unfortunately, the simultaneous occurrence of rotational and translational optic flow is potentially confusing to the visual system, and rotational optic flow is unavoidable when turns must be made to change course. Although untangling the two types of optic flow is possible in principle (Longuet-Higgins and Pradny, 1980; Koenderink, 1986), this may not always be feasible if there is noise in the signals and if the neurons are noisy and have a limited dynamic range available for their responses. In this case, the strategy followed by the blowfly may be a superior one: the rotational optic flow is concentrated at specific points in time (the saccades), allowing the remaining time to be used for analyzing the structure of the visual environment on the assumption of translatory optic flow only.

The shortening of the yaw saccade of the head compared with that of the thorax can be viewed as a further specialization

to increase the time available for scene analysis (Schilstra and van Hateren, 1998b). The saccade becomes effectively almost as short (for the smallest saccades only a 15–20 ms period of significant visual blur) as the integration time of the photoreceptor (10 ms for the conditions of the experiment). Saccades much shorter than the integration time are disadvantageous, because they do not reduce visual blur further and are energetically more costly because of the higher accelerations (and therefore forces) required.

Between saccades, several systems are acting to stabilize the gaze (Hengstenberg, 1992), such as the prosternal organs on the thorax (Preuss and Hengstenberg, 1992), visual feedback through optic flow analysis (Egelhaaf and Borst, 1993; Krapp and Hengstenberg, 1996) and a mechanical system of gyroscopic sensors attached to the thorax, the halteres (Nalbach, 1993; for a recent overview, see Chan et al., 1998). The visual system, however, is too slow to explain the angular stability of the head at the onset and end of a saccade (e.g. the latency of the photoreceptors alone is 8 ms at the light levels of the experiment). It is possible that the thorax and head movements during a saccade are entirely preprogrammed on the basis of predicted flight dynamics. A more likely possibility, however, is that head stabilization at early and late stages of the saccade is controlled by the halteres. This analogue of the vestibulo-ocular reflex in vertebrates (see, for example, Tabak et al., 1997) has been demonstrated in experiments in which mechanical stimulation of the halteres induces head movements (Sandeman and Markl, 1980) with a minimum latency of approximately 5 ms (Hengstenberg et al., 1986). We propose the following scheme: early in the saccade, the haltere–head reflex causes the head rotation that compensates for the early stages of the thorax saccade. Subsequently, the haltere–head reflex is suppressed or overruled, and the head makes its saccade (with the size and direction under the control of the brain, which also initiated the preceding thorax saccade). Finally, the haltere–head reflex becomes dominant again towards the end of the head saccade, producing the final counter rotation of the head.

The oscillations found in the pitch of the head appear to be genuine, although influenced by the mass of the coils mounted on the head. The amplitude of the oscillation ($0.35 \pm 0.08^\circ$ peak-to-peak) is much smaller than the angular sensitivity of single photoreceptors (approximately 1.5° full width at half-maximum; Smakman et al., 1984). This amplitude will nevertheless produce a significant intensity modulation when an edge or bar happens to cross the visual field of the photoreceptor. The frequency of this modulation (typically 120–170 Hz) is rather high for blowfly photoreceptors (with an integration time of 7 ms in very bright light), which significantly reduces the resulting modulation. Thus, the pitch oscillation will not have a strong visual effect on single photoreceptors. The situation is different, however, for wide-field neurons: because the head oscillation affects the entire visual field simultaneously, a noticeable effect is expected when the signals from many photoreceptors converge. This assumes that the contributions of brightness increments and

decrements over the visual field do not cancel, because this is prevented by nonlinearities in the signal pathways before they converge.

The present method records head movements and infers gaze direction from the orientation of the head. Although the facet lenses of the compound eye are fixed to the head, the photoreceptors in blowflies are not completely fixed relative to the facets. Through several muscles, small movements of up to a few degrees can be made by the photoreceptors relative to the head (Hengstenberg, 1971; Franceschini and Chagneux, 1997). A visual function for these movements has been proposed (Franceschini and Chagneux, 1997). Because these movements are generally small and slow compared with the saccadic head movements described in the present study, we believe that these internal retinal movements are, at most, a second-order effect compared with the head movements during saccades.

The histograms in Fig. 6 show that the angular velocities of the head between saccades are generally lower than $100\text{--}200^\circ\text{ s}^{-1}$. This is well matched to the velocity at which blur in the photoreceptors becomes important. This so-called characteristic velocity, v_c (van Hateren, 1992a; see also Glantz, 1991), is $\Delta\rho/\Delta t = 200^\circ\text{ s}^{-1}$, with the full width at half-maximum of the photoreceptor angular sensitivity $\Delta\rho \approx 1.5^\circ$ and that of the photoreceptor impulse response $\Delta t \approx 7\text{ ms}$. Nevertheless, this is only part of the story, because this analysis only gives the blur attributable to rotation. The blur attributable to translation has to be accounted for as well. This blur can be determined from a reconstruction of the complete spatiotemporal input to the eye, taking into account both the animal's time-varying position and orientation and the visual stimuli on the walls of the cage. Such a study is currently under way.

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